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SHORTER ARTICLES AND DISCUSSION

STUDIES ON INBREEDING. VIII. A SINGLE NUMERICAL MEASURE OF THE TOTAL AMOUNT OF INBREEDING[1]

1. In the earlier numbers of these Studies, and particularly in VII,[2] methods have been given for measuring the amount or degree of inbreeding exhibited in a particular pedigree by a series of inbreeding coefficients, $Z_1, Z_2, Z_3, \ldots, Z_n$, one for each ancestral generation. The inbreeding for the whole pedigree is indicated by an inbreeding curve, formed by plotting and connecting by a line the several coefficients.

2. From the earliest stages of this investigation the writer has been aware of the desirability of a *single* numerical measure, to supplement or replace the inbreeding curve as a designation of the total inbreeding exhibited. Such a designation has now been found, which, it is believed, uniquely and rigorously meets the requirements. It is the purpose of the present paper to describe this new constant.

Consider Fig. 1. This gives, in the heavy line and solid circles, the inbreeding curve for 9 ancestral generations of the Brown Swiss bull, Saxton (2668).[3] The values of the inbreeding coefficients are:

$$Z_1 = 0, \qquad Z_4 = 12.50, \qquad Z_7 = 26.95,$$

$$Z_2 = 0, \qquad Z_5 = 17.19, \qquad Z_8 = 28.91,$$

$$Z_3 = 6.25, \qquad Z_6 = 21.09, \qquad Z_9 = 29.30.$$

The smooth curve of Fig. 1 is the inbreeding curve for continued brother × sister mating. This represents the closest or maximum degree of inbreeding possible in sexually reproducing organisms.

It is clear from inspection of this diagram, that Saxton is much less intensely inbred in fact than he would be if in all his ancestry the matings had been of brother × sister out of brother

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[1] Papers from the Biological Laboratory of the Maine Agricultural Experiment Station. No. 118.

[2] Pearl, R., AMER. NAT., 1917, in press.

[3] Cf. Pearl, R., these Studies, I. AMER. NAT., Vol. XLVII., p. 603, 1913.

× sister, etc. This is evident, in the first place, because the ordinates of the Saxton curve, *a c* are nowhere as high as those of the brother × sister curve, *a b*. But it would also be equally clear that Saxton was less inbred than the maximum possible amount if the last ordinate at *c*, for example, had a value of 99.6, as does the corresponding ordinate of the maximum curve.

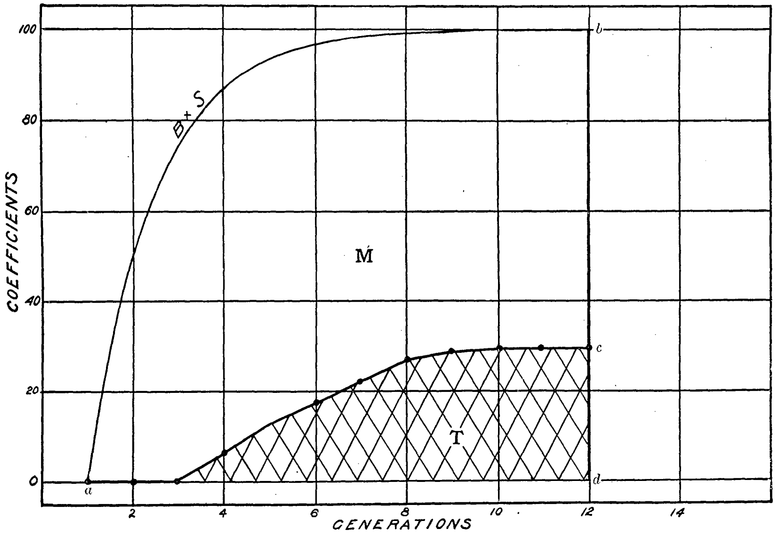

FIG. 1. Diagram showing the inbreeding curve of Saxton, a Brown Swiss bull, in the heavy lines and solid circles. The smooth, light line curve is the curve of maximum inbreeding (continued brother × sister breeding). For further explanation see text.

Upon consideration it appears that the real measure of comparative amount or degree of inbreeding, considering the pedigree as a whole, is given by the *area* included by the particular inbreeding curve under discussion, as compared with the corresponding area of the maximum (brother × sister) curve. Thus in Fig. 1, Saxton is less inbred than the maximum possible amount to an extent proportionate to the amount by which the area *T* (*a c d*) is smaller than the area *M* (*a b d*). This consideration gives us the desired method of uniquely expressing the total amount or degree of inbreeding. It only remains to consider practical methods of calculation.

3. Theoretically one should integrate the maximum (brother × sister) curve, and the observed curve, and compare the areas derived from such integrations. Practically this is not possible, because many observed curves of inbreeding can not be fitted by

any simple, readily integrable theoretical curves. We shall hence be compelled in this case to make use of the expedient so frequently employed in applied mathematical problems of all sorts, namely, to take finite summation as a sufficiently close approximation to integration. Doing so, we may take as the simple expression of total inbreeding, to and including the nth generation, the following:

$$\frac{Z_{T_n}}{100}=\frac{\Sigma_{Z_1}^{Z_n}}{F_{T_n}}, \tag{i}$$

where Σ denotes summation of all values between the inclusive limits indicated, and F_{T_n} is a constant having the value set forth in Table I. F_{T_n} is of course the total area of the maximum brother × sister curve up to and including the $n+1$-th generation. Since these successive values are constant they may be tabled once for all.

TABLE I

VALUES OF F_{T_n}, THE INCLUSIVE AREAS OF THE MAXIMUM INBREEDING CURVE

Ancestral generation	n	F_{T_n}
2	1	50
3	2	125
4	3	212.5
5	4	306.25
6	5	403.125
7	6	501.5625
8	7	600.78125
9	8	700.390625
10	9	800.1953125[4]
11	10	900.09765625
12	11	1000.048828125
13	12	1100.0244140625
14	13	1200.01220703125
15	14	1300.006103515625
16	15	1400.0030517578125

In using the form of total inbreeding coefficients shown in (i) there is one caution which must be carefully observed. This is that only so many generations should be used as to include the one in which the observed Z taken first reaches its highest value for the pedigree under discussion, and not any beyond that one. This will usually be for the earliest ancestral generation of the pedigree, but not always.

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[4] One would not, of course, use in practical calculation such excessive numbers of decimals as are tabled from this point on.

4. We may now consider some numerical illustrations. Let us take first the bull Saxton, for which the several observed inbreeding coefficients have already been given. We have

$$\Sigma_{Z_1}^{Z_9} = 142.19$$

and hence, from Table I,

$$Z_{T_9} = \frac{14219}{800.1953} = 17.8.$$

Or we may say that Saxton is inbred in ten ancestral generations, taken together 17.8 per cent. of the maximum amount possible in those generations.

For comparison some other figures may be examined. Pearl and Patterson[5] have given mean values of the inbreeding coefficients for four groups of Jersey cattle: (*a*) Random sample bulls, (*b*) register of merit bulls, (*c*) random sample cows, (*d*) register of merit cows. It will be of interest to reexamine these figures by the method here described. The results are given in Table II.

TABLE II

TOTAL INBREEDING COEFFICIENTS FOR JERSEY CATTLE. (PEARL AND PATTERSON DATA)

Group	Total Inbreeding Coefficients Z_{T_7}		
	Lower Limiting Values	Upper Limiting Values	Mean
1. General population (random sample) bulls	25.39	30.48	27.94
2. Register of merit bulls	24.52	29.17	31.85
3. General population (random sample) cows	27.46	31.74	29.60
4. Register of merit cows	20.72	27.08	23.90

From this table we see that American Jersey cattle, as judged by random samples of the general population, are about 28 to 30 per cent. as closely inbred as the maximum possible amount, taking account of the first eight ancestral generations *as a whole*.

It is not desirable to go further into the discussion of these Jersey data, since the purpose of this note is simply an exposition of method. This new method makes possible exact and unique numerical comparison between pedigrees in respect of the degree of inbreeding which they exhibit in the same number of ancestral generations.

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[5] Pearl, R., and Patterson, S. W., *Proc. Nat. Acad. Sci.*, Vol. 2, p. 60, 1916.